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Ecosystem theory and management[1]

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Introduction

In Western Australia, and particularly in the vicinity of Perth, man and his activities are producing a serious impact on the remaining natural ecosystems so that it is both prudent and desirable to intervene and manage them in order that further undesirable changes are avoided or reduced.

Adequate management of ecosystems requires a prescription for action which has a basis in a theory of how ecosystems function. However, ecosystems are naturally so complex that it is necessary to dissect them into component parts or processes for analysis. Thus study may be devoted to the chronological development of the ecosystem, or the diversity or complexity of the ecosystem, or competitive relationships within a community, or community structure (producer/consumer or predator/prey interactions). While these studies give insights into interactions, they throw little light on processes operating with communities which in turn are related to diversity, complexity and stability. These lie at the core of any understanding which can form the basis for management. Recent studies emphasise the structural components of ecosystems, e.g. species, while overlooking the other aspects of ecosystems, namely, the processes involved, especially their role or function, and it is this aspect that I propose to emphasise in the following brief development of a theory of how ecosystems might be integrated, and then apply the theory in a suggestive way to the local scene.

In order to construct a general theory I propose to take as a starting point the observation that life depends on the fixation of nitrogen and the elaboration of biologically complex molecules which can only be done by a limited variety of organisms. Once elaborated, these molecules are a resource to be exploited by organisms which cannot elaborate them. It is the pattern of elaboration and exploitation that constitutes the functional aspects of the ecosystem or community. That is, the construction of the theory relies on a biological approach which takes into account diversity, complexity and stability which earlier I suggested were near the core of understanding ecosystems.

Diversity

Taking the elaboration of biologically essential molecules as a starting point, it is possible to conceive or construct a hypothetical community in which the biological molecules enter the system by way of synthesisers and have a residual time in the community, which is related as an

$$\text{input}—\left\{\begin{matrix}\text{synthesis;}\\ \text{dinitrification}\\ \text{photosynthesis}\end{matrix}\right\}—\!\!>\text{output}—\left\{\begin{matrix}\text{biological}\\ \text{degradation}\end{matrix}\right\}$$

system. The nitrogen fixed and the molecules synthesised are a resource to be exploited by organisms unable to synthesise them themselves. Without the interpolation of exploiting organisms a system could be conceived of as producers and degraders (bacterial decomposition). Without exploiting organisms the system is at its simplest when the most vigourous and actively reproducing and growing synthesiser outcompetes others for space and other resources. Diversity of producers will be increased when a fluctuating environment alternatively favours the fundamental niche (Hutchinson 1957) of one or the other of the synthesisers; or when exploiting organisms assume the role of predators of the synthesiser, the predators being favoured or not according to the way environmental changes exceed or otherwise the possible states of persistence defined by their fundamental niche; or when competitive interactions delimit the realised niche of some of the synthesisers or predators. By a combination of these interactions it is possible to go on packing the community with producers and consumers until the resources of space, nutrients, and biologically useful molecules can be divided no further and still support an exploiting population.

In this sense the variety of consuming organisms interpolated between the synthesisers and the degraders is a device for delaying the ultimate degradation of biological material by bacteria or increasing the residence time before ultimate degradation.

Complexity

The basis of the community is nitrogen fixation and the producers of biologically useful molecules, particularly amino acids and carbohydrates. The most easily measured of these basic entities are those concerned with trapped solar energy, that is, carbon flow. However, the flow of biologically useful nitrogenous compounds can be conceived as being of extreme importance since nitrogen is essential for growth and the nitrogen pool of the system could conceivably be more limiting than any ability to synthesise carbohydrates. The pool is of course replenished by nitrogen fixation, and in the Australian ecosystems there may be anaerobic prokaryotes, photosynthesising prokaryotes, lichens, rhizobial symbionts on legumes, or actinomycete symbionts on other plants, e.g *Casuarina*. Not all these routes of fixation operate all the

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time: some are limited by seasonal conditions; others are limited by seral stages in plant succession, e.g. legumes in post-fire regeneration, or by the availability of decomposing litter as an energy source for both aerobic and anaerobic nitrogen fixers.

Since the components of a community cannot grow without amino acids and the nitrogen of the pool depends on fixation, on the average at least replacing that lost from the system by decomposition, then the certainty that some nitrogen fixation will occur will be related to the array of modes in the pathways of nitrogen fixation.

The probability of persistence of the community approaches 1 when the route or pathway diversity is such that there will always be one mode operating under all experienced variations of the environment. Such a condition of diversity would define stability with respect to the nitrogen needs of the ecosystem, i.e. leaks from the system could be replaced by addition to the pool by fixation under all perturbing conditions.

Mineral nutrients are also essential and often limited in supply. Recycling of these nutrients increases their retention time in the system. The pool is replaced by release of pollen, flowering, fruit and seed of deep-rooted plants which gather nutrients from deep weathering profiles or from accumulations of resulting downward leaching of soil solutes. Usually there is more than one route for replenishment of the mineral nutrient pool. In a post-fire situation the loss of mineral nutrients from the system by run-off and rainfall is minimised by the harvest by the root system of freshly grown underground bulbs and tubers and rhizomes or by shrubs with lignotubers or by mycorrhizal fungi. Again there are a number of ways for blocking leaks from the system. Leakage will be least when the diversity of ways of gathering the nutrients released in the post-fire situation is such that at least one route will operate under any conceivable post-fire situation.

In addition to the pathways of fixation there is a tendency for nutrients to accumulate at their place of origin or to fall into sinks, e.g. bogs, lakes, the water table, or even in long-lived vegetation and deep-rooted plants. Herbivores and predators can be looked upon as devices for redistributing these nutrients.

In the sense used here, complexity has to do with variety of modes in the pathways by which biologically important materials are introduced into the system, the different modes of retention and storage, and the ways in which they are redistributed.

Stability

In the foregoing examples diversity and complexity have related to (i) maximising the retention time of expensive biological molecules within a system, and (ii) diversifying the number of modes in routes by which the pool of biologically useful nutrients is introduced into, retained, and redistributed within the system so that a supply and retention is ensured under all possible or conceivable circumstances.

In this sense the community that persists through perturbations or disturbances is successful at achieving diversity in supply and retention and has thereby achieved stability.

At any one instant of time one mode in a route may be more important or efficient than another. At such a juncture the inefficient routes are redundant but stability on a long-term basis may in fact be dependent on the retention of the redundancies. They are in effect insurance policies. Efficiency of use of a resource enhances the retention time by minimising loss through the production of biologically useless degradation products. However, as mentioned earlier, over a long period of time "sinks" will appear within a system and nutrients will accumulate there. Ultimately there will be areas rich in nutrients and others poor in nutrients. In the sense of preserving a community it is advantageous to delay this end, and we can consider mobile animals as devices which delay this end state. Animals such as chironomids or frogs emerging from ponds or moth or other insect larvae from trees or bees distributing pollen or mating flights of ants or termites, or herbivores or predators generally, are to be viewed as devices for delaying the accumulation or redistributing important biological substances.

Management

The problems of management range from the problems associated with natural communities which are being distributed by being isolated as small reserves or invaded by pathogen (*Phytophthora*) to the situations which are physically disturbed such as road verges, or pits left by gravel extraction or bauxite mining. In such disturbed places, a new community may establish but it would take a long time. Nutrients could be added and so hasten the establishment of vegetation—but there is no feed-back if nutrient supply is unbalanced. Moreover, from the theoretical framework developed, the nutrients may have to be replenished repeatedly if the community diversity and complexity necessary for their retention is not present, and replenishment is likely to be a costly and continuing process unless the natural input to the nutrient pool can be balanced with the losses from the pool by means of a suitably diverse and complex community. Finally, stability will only be achieved when supplying pathways are assured under all natural perturbations.

Discussion

In the foregoing I have emphasised that diversity of roles is essential so that retention times of nutrients or replenishment of nutrient pools is maximised under all possible circumstances. Establishment of roles is hard work requiring a great deal of biological insight. However, in addition to the well-known ability of symbionts associated with legumes to fix nitrogen, there is now an extensive and growing literature on nitrogen fixation by plant associations other than with legumes (Silvester 1977) as well as by free-living microbes (Postgate 1971). Of particular interest is the ability of actinomycete symbionts associated with *Casuarina* to fix nitrogen. Actinomycetes appear to be capable of establishing symbiotic relationships with a number of woody shrubs (Silvester 1977) and there may be as yet unrecorded symbioses among the endemic woody shrubs. Shea and Kitt (1976) have indicated the levels of nitrogen fixation by native legumes, while Halliday and Pate (1976) have shown that blue-green algae associated with *Macrozamia* are capable of contributing nitrogen to their host.

Peculiarities of the root systems of Australian Proteacea have been studied for some time (Specht and Rayson 1957, Purnell 1960). Lamont (1972a, b, 1973) has made a detailed study of the proteoid roots of some *Hakea* species, while Lamont and McComb (1974) have studied the role of microorganisms in the formation of proteoid roots and Jeffrey (1967, 1968) has implicated the importance of proteoid roots in phosphorus nutrition.

Additionally fungi are being more and more implicated as important components of ecosystems, both as decomposers and in mycorrhizal associations (Hartley 1959, 1971). Moreover, mycorrhizas are associated with eucalypts (Chilvers and Pryor 1965) and may well be more widespread. Malajczuk *et al.* (1977) have experimentally demonstrated the importance of mycorrhizal infection. Mycorrhizas appear to be important in increasing the area through which solutes can be absorbed. They thus could have an important role in retaining mineral nutrients within the ecosystem, especially where soils are sandy and lack clays on which nutrients might be absorbed and thus physically retained.

The foregoing suggests that natural history observations such as the invasion of gravel pits by *Dryandra* rather than legumes or the invasion of disturbed sandy areas or sand pits on the Swan coastal plain by *Adenanthos* are in some way related to the role of proteoid roots in nutrition. Likewise the ubiquity of *Casuarina* species among the vegetation associations growing on poor sandy soils could indicate the common mode of nitrogen fixation in the system.

Taken together the above suggest that in addition to establishing the roles played by plant species we need also to pay much more attention to the microorganisms of the soil, i.e. the rhizosphere, as well as those that are symbionts on woody plants.

The identification of multiple modes in pathways by which biologically useful materials are introduced into a system, and an assessment of the conditions under which each is optimised, have not been attempted. Nevertheless if segments of the system can be isolated, it is possible in theory to establish measures of species diversity for the different pathways, and ideally measure the contribution of each of these to the circulating pool of biologically important substances. Moreover, it may be possible to establish the robustness of components of these pathways under perturbation. For example, when perturbations occur, there are a number of characteristic sequences for regeneration, as already mentioned: Proteacea *(Dryandra)* but generally not legumes in gravel pits where soil and accumulated nutrients are in poor supply, or legumes in burnt areas where, depending on the intensity of the fire, nitrogen but not minerals will be depleted. Perhaps these characteristics in successional sequences are a manifestation of dominant pathways by which limiting nutrients are being restored to the system.

Thus whilst diversity contributes to the retention time of biologically expensive nutrients in an ecosystem, it is likely that it is the multiplicity of modes in pathways (duplications or redundancies) by which biologically useful molecules are introduced into (blue-green algae, lichens, free-living aerobic and anaerobic microbes, symbiotic actinomycetes and symbiont rhizobia) or retained within (fungi, mycorrhiza, proteoid and other root systems, geophytes and lignotubers which can rapidly produce an extensive root system to scavenge and retain nutrients) the ecosystem which is important for stability of the system. The suggestion is that these redundancies are such that in a stable system at least one mode in each pathway will operate under the conditions of perturbation natural to the system, and natural history observations may give a first clue to the robustness of each mode.

The generalisation for the above example is that under perturbations induced by gravel extraction where depletion of soluble phosphorus is presumed, the phosphorus replenishment mode by way of proteaceous plants is robust, while the nitrogen mode by way of leguminous plants is not. On the other hand, following burning, when the phosphorus pool is intact and the nitrogen pool depleted, the mode of nitrogen fixation by way of symbionts in legumes is robust.

In a community disturbed by the invasion of *Phytophthora*, or where any other cause of catastrophic destruction of vegetation occurs, diversity and complexity are destroyed and no mode in any pathway persists, hence stability is lost.

Management should take into account these functional roles of diversity and complexity, but it is not likely to be easy to develop a complete data base since so much of importance takes place in the rhizosphere.

In summary, the theory developed is based on functional integrity of the ecosystem rather than specific components at any time. It has been assumed that a system cannot sustain itself unless nitrogen is fixed and minerals introduced into the system in quantities which equal losses from the system. Should these biologically important substances be in excess of what the system can use they will be lost, i.e. the system will leak. The presence of a substantial leak suggests that there is an unexploited resource which could be exploited by an organism new to the system. Should this happen, the leak will be stopped and the diversity of the system increased. The assumption is that diversity increases until all serious leaks are stopped.

In addition, the theory suggests that because environments fluctuate seasonally, and suffer other types of perturbation and disturbance, only those persist which contain a variety of modes in the pathways by which biologically important substances are introduced and retained within the system. The variety of modes reflects the complexity of the system. Frequently there are redundancies in modes but functionally the system retains its integrity and tends to return to its former state after perturbations or disturbances. It is the robustness of pathways which endows the ecosystem with stability.

In terms of management of the ecosystem, the compartments that appear to be important are those devoted to the accession of nutrients; the synthesisers (fixation of nitrogen, extraction of mineral nutrients from deep profiles and photosynthesis); the redistribution of nutrients (the animal component of the ecosystem); and the organisms which maximise retention of nutrients within the system (fungi, mycorrhizas and plant root systems generally).

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